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Morphological changes in kleptochloroplasts after ingestion in the unarmored dinoflagellates

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Dinoflagellates are ubiquitous unicellular protists and the evolutionary scenario of their chloroplast evolution is quite complex one. About half of the dinoflagellates are photosynthetic, while rests are heterotrophic species, and the latters are thought to have evolved from the photosynthetic ancestors by losing their chloroplasts. Additionally, some dinoflagellates have replaced their original chloroplasts with those of haptophyte, diatom or green alga. In addition, some dinoflagellates possess 'kleptochloroplast', which is the temporary chloroplast 'stolen' from other photosynthetic algae.

The unarmoured dinoflagellate *Amphidinium poecilochroum* (marine) and *Gymnodinium aeruginosum* (freshwater) are closely-related to each other, and both possess kleptochloroplasts derived from cryptomonads. These dinoflagellates ingest cryptomonad cell and retain its chloroplast temporarily, but eventually lose the chloroplast due to cell division or digestion. Previous studies revealed that several differences exist between marine and freshwater representatives with regard to the cryptomonad-dinoflagellate specificity and the dynamics of kleptochloroplast processing. *A. poecilochroum* is capable of ingesting any species of cryptomonads, and synchronised division of kleptochloroplast with the host cell has never been observed. By contrast, *G. aeruginosum* can accept only members of the genus *Chroomonas* as prey and the kleptochloroplast is simultaneously divided with the host cell and being inherited by each daughter cell. Thus, the kleptochloroplastidy in *G. aeruginosum* seems to represent much more advanced stage toward acquisition of 'true chloroplast' within the linage. Therefore, unraveling the differences between the two species in detail might give us clue to understand evolutionary significance and contribution of kleptochloroplast during the quest for true chloroplasts. Although the general ultrastructure of these dinoflagellates has been studied, the morphological changes from ingestion of cryptomonad to disappearance of kleptochloroplast have never been focused and remain unclear. In this study, we observed the morphological changes of kleptochloroplast in *A. poecilochroum* and *G. aeruginosum* using light and transmission electron microscopes, and compared the differences between the two species.

The both species ingested cryptomonad chloroplast, nucleus, nucleomorph, mitochondria and ejectosomes with surrounding cytoplasm directly into the dinoflagellate cytoplasm. In *A. poecilochroum*, cryptomonad mitochondria and ejectosomes were removed together with cytoplasm, by transferring them into the food vacuole within 1 h after ingestion. The kleptochloroplast was enlarged gradually, and the cryptomonad nucleus was digested after 3 h. In *G. aeruginosum*, the cryptomonad cytoplasm, containing cryptomonad nucleus and mitochondria, was retained around the chloroplast. The chloroplast was enlarged drastically after 6 h, and eventually occupied most of the host cytoplasm by the 3rd day, forming a cup shape with several pyrenoids. The cryptomonad nucleus was positioned inside the cup-shaped chloroplast. By the day 5, the nucleomorph has undergone multiplication at the vicinity of the cryptomonad nucleus. This study revealed that *G. aeruginosum* can expand its kleptochloroplast more extensively and is capable of retaining the cryptomonad nucleus for a longer period than *A. poecilochroum*. Previous study on the kleptochloroplastidic ciliate *Mesodinium rubrum* showed that the endosymbiont nucleus plays an important role to maintain its kleptochloroplast. The diatom-harboring dinoflagellates possess diatom nucleus, and can divide the latter nucleus simultaneously with the host cell division. The differences between *G. aeruginosum* and *A. poecilochroum* indicated in this study also support that retention of endosymbiont nucleus is advantageous to maintain its chloroplast stably.

Keywords: dinoflagellate, kleptochloroplast, ultrastructure